

Evidence for Host Plant Preferences in *Heliconius erato phyllis* from Southern Brazil (Nymphalidae)

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Abstract. The oviposition behaviour of female *Heliconius erato phyllis* was investigated in relation to 9 species of host plants belonging to the genus *Passiflora*. Larvae were reared on the same host plants to assess their viabilities, rate of development from eggs to pupae and pupal weights. Results indicate that the subspecies *phyllis* is oligophagic with an incipient specialization on *Passiflora misera*. Some results imply that plant abundance does not play a primary role in this specialization.

Introduction

Since Ehrlich and Raven's (1964) original article, the literature on coevolution of butterflies and plants has increased substantially. Among the most intensely studied groups of butterflies, are the Pieridae (see for instance Chew, 1977), Papilionidae (Rauscher, 1980; Rauscher and Papaj, 1983; Berenbaum and Feeny, 1981, among others) and Nymphalidae, particularly the tribe Heliconiini (a comprehensive treatment can be found in Benson, Brown and Gilbert, 1975). Few of these studies, however, investigate how coevolution between butterflies and plants originates; although relevant in this context is the work of Smiley (1978a, b) with three species of *Heliconius* from Costa Rica, where the primary determinants of monophagy were tested, the ecological factors predation and plant abundance as well as host palatability. This investigation contributes with additional data testing larval development parameters for the butterfly *Heliconius erato phyllis* on nine species of *Passiflora*. A brief consideration of adaptive strategies involved is also presented.

Materials and Methods

Adult *Heliconius erato phyllis* butterflies used in this study are from Rio Grande do Sul, the southernmost state of Brazil with both subtropical and temperate climate. This species is widespread, the populations exhibiting marked oscillations through the year, and local extinctions have been recorded (Saalfeld and Araújo, 1981; Pansera and Araújo, 1983). Sixteen females were used in oviposition tests, 12 from the wild and 4 from insectary matings. The species of *Passiflora* tested

were: *P. misera*, *capsularis* and *suberosa* belonging to the subgenus *Plectostemma*; *coerulea*, *elegans*, *alata*, *tenuifila*, *edulis* and *actinia*, subgenus *Granadilla*. These are 9 of the 13 available species in Rio Grande do Sul (Sacco, 1962, 1980) and include all those frequently used by *H. erato phyllis* in nature.

The experimental procedure followed two steps: in the first, females were isolated from passion-flowers for 48 or 96 hours. They then were offered pots with fresh plants on which to oviposit, one *Passiflora* species at a time. Because the results for the two isolation intervals were not significantly different, they were combined. Each test lasted 30 minutes, the female having 2 or 3 pots of the same species to oviposit. All the oviposition behaviour was carefully observed and the host acceptability ratio (H.A.) measured as the No. of tests with oviposition/No. of tests with foretarsal drumming behaviour. In order to quantify the preference for each host plant we calculated an oviposition rate (O.R.) as the No. of eggs/No. of tests with oviposition.

The second step involved feeding caterpillars until pupation on a single species of host plant. Eggs collected in nature or in the insectary were removed from the plant, weighed and placed individually in plastic vials in a controlled temperature chamber at 25°C. Larval growth was measured following the procedures of Smiley (1978b). For statistical analysis the data were transformed in natural logarithms.

Results and Discussion

Table 1 shows the results for oviposition ratio and index of preference of *H. erato phyllis* on the nine species of *Passiflora*. Three groups of host plants can be roughly distinguished concerning H.A.: those with high values (*P. capsularis* and *misera*), those with moderate, about fifty per cent oviposition (*P. alata*, *edulis*, *suberosa* and *coerulea*), and those with low values (*P. actinia*, *elegans* and *tenuifila*). Interesting to note is that if

Table 1. Host acceptability (H.A.) and oviposition rate (O.R.) in nine species of *Passiflora*.

Passiflora		H.A. (%)	O.R.
<i>capsularis</i>	(20)	100	1.3
<i>misera</i>	(27)	90	2.5
<i>alata</i>	(13)	60	1.5
<i>edulis</i>	(17)	57	1.0
<i>suberosa</i>	(16)	50	1.7
<i>coerulea</i>	(17)	50	1.2
<i>actinia</i>	(20)	33	1.0
<i>elegans</i>	(12)	0	0
<i>tenuifila</i>	(10)	0	0

() = number of tests made

one looks at the O.R. for the same plants there is relatively poor correlation; for instance, it is greater for *P. misera*, followed by *suberosa* and *alata*, only then by *capsularis*. Observations suggest, however, that the results here reported are similar to oviposition in the field near Porto Alegre, Rio Grande do Sul; we have found, whenever *P. misera*, *coerulea* and *elegans* are present in the same area, that eggs are found almost only in the first species. In other areas where *P. coerulea* is replaced by *suberosa*, the proportion of eggs on the latter is found to increase. In the Northwest of the State, where *P. tenuifila* is abundant, one of us (AMA) found only one egg in that plant during almost four years of observations!

The proportion of eggs reaching adulthood (egg to adult viability), the development time from egg to pupa and larval growth rates are presented in Table 2 and Figure 1. *P. suberosa* showed the highest percentage of viable adults, followed by *P. misera* and *capsularis*. *P. tenuifila* and *alata* were lethal to feeding larvae, while on *P. edulis* only 13% of eggs became adults (interestingly these last two species release great amounts of HCN when macerated—K.S. Brown, Jr., pers. comm.). The next two columns in the table are correlated; *P. misera* seems to be the most nutritious among species tested, caterpillars fed with it pupate after an average of 12 days. The results obtained for *P. elegans* are surprising since its mean exceeded

Table 2. Viable adults, development egg-pupa (mean \pm S.D., days) and larval growth rates (mean \pm S.D.) for different species of *Passiflora*.

Passiflora	No. of eggs	Viable adults n	Viable adults %	Development egg-pupa	Larval growth rate
<i>capsularis</i>	19	14	73	16 \pm 1.7	0.72 \pm 0.10
<i>misera</i>	72	54	75	12 \pm 1.0	1.02 \pm 0.13
<i>alata</i>	39	0	0	0	0
<i>edulis</i>	15	2	13	18 \pm 3.6	0.59 \pm 0.14
<i>suberosa</i>	54	48	88	15 \pm 2.5	0.81 \pm 0.12
<i>coerulea</i>	5	3	60	24 \pm 4.6	0.47 \pm 0.10
<i>elegans</i>	62	26	41	14 \pm 1.9	0.87 \pm 0.08
<i>tenuifila</i>	37	0	0	0	0

Passiflora actinia was not tested due to shortage of plants available for feeding caterpillars.

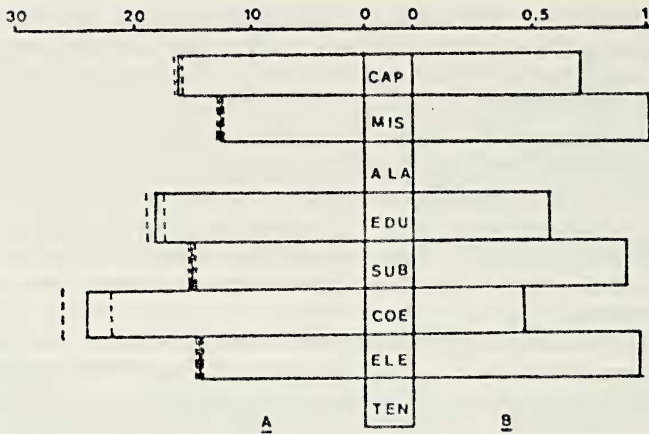


Fig. 1. Graphical representation for development egg-pupa (A) (days), and larval growth rate (B). Hatched lines indicate standard errors. Species of *Passiflora*: CAP = *capsularis*; MIS = *misera*; ALA = *alata*; EDU = *edulis*; SUB = *suberosa*; COE = *coerulea*; ELE = *elegans*; TEN = *tenuifila*.

only two days that for *P. misera*. Considering that *P. elegans* is very common in some localities, collocated with *P. misera*, but is rarely used, we might conjecture that here there is an indication of palatability (or digestive efficiency) being precedent to an ecological factor (plant abundance). The same can be said of the *P. misera* and *suberosa* comparison. At Itapuã, near Porto Alegre, both species are equally common (Saalfeld and Araújo, 1981); nevertheless, eggs are found more frequently on *P. misera*. Another suggestion of palatability being precedent is the fact that *P. capsularis* and *tenuifila*, occurring abundantly at the Parque do Turvo show a remarkable difference in oviposition, that is, females prefer to lay eggs on *P. capsularis* instead of on *P. tenuifila* (this latter species was lethal in our experiment).

An analysis of variance carried out to test the equality of mean number of days for development from egg to pupa, and the mean pupal weights obtained for caterpillars fed with *P. misera*, *capsularis*, *elegans* and *suberosa* are shown in Table 3 (untransformed values for the latter parameter were: *P. misera*, 357 ± 31 mg; *P. capsularis*, 254 ± 80 mg; *P. elegans*, 329 ± 52 mg; *P. suberosa*, 325 ± 45 mg). For both variables the F-test showed highly significant results. However, when a partition of the "sum of squares between" is made, complementary results are obtained. So, if the mean number of days for development egg to pupa is considered, the comparison *misera* \times *elegans* showed a significant difference, while the other two comparisons did not. If, on the other hand, mean pupal weight is taken into account, the only significant difference is that between *sub-*

Table 3. Analysis of variance for differences in development egg-pupa (a) and pupal weight (b). Original data transformed in $\ln x$.

	Source of variation	SS	DF	MS	F
(a)	Between	1.2423	3	0.4141	20.10 ***
	(mis x ele)	0.2905	1	0.2905	14.10 ***
	(ele x sub)	0.0651	1	0.0651	3.16 n. s.
	(sub x cap)	0.0298	1	0.0298	1.45 n.s.
	Within	2.8028	136	0.0206	
(b)	Between	0.5746	3	0.1915	7.85 ***
	(mis x ele)	0.0663	1	0.0663	2.72 n.s.
	(ele x sub)	0.0021	1	0.0021	0.09 n.s.
	(sub x cap)	0.2539	1	0.2539	10.40 ***
	Within	3.3216	136	0.0244	

*** = $P < 0.001$

n.s. = non significant

erosa × *capsularis*. On the basis of such analysis one can make the following scheme, where species united by a bar have equal means:

Development egg to pupa (days)

Numerical values ***misera* < *elegans* < *suberosa* < *capsularis***

Statistical tests

Pupal weight (mg)

Numerical values ***misera* > *elegans* > *suberosa* > *capsularis***

Statistical tests

Conclusions

The results here reported allow the following conclusions to be made: 1. *Heliconius erato phyllis* from the Southern Brazil is an oligophagic species; moreover, the *Passiflora* host plants preferred belong to the subgenus *Plectostemma*, supporting the findings of Benson et al. (1975). It is interesting to note that another *H. erato* subspecies, *petiverana*, has developed an specialization already, being classified as monophagic (Smiley, 1978b). 2. Caterpillars fed with *Passiflora misera* had the fastest development time from egg to pupa, suggesting a certain amount of digestive specialization. Since *H. erato phyllis* has a wider distribution than

this plant we believe this specialization to be a recent phenomenon. 3. As some of the *Passiflora* in this study are as abundant as *P. misera* in the area sampled (particularly *P. suberosa* and *P. elegans*) it seems that plant abundance does not represent the primary factor for specialization. 4. For the two variables presumably related to fitness (rate of development from egg to pupa, and pupal weight) the results obtained when caterpillars are fed with *P. misera* indicate that, as far as speed of development is concerned, *H. erato phyllis* in Rio Grande do Sul can be viewed as an opportunistic species, since in a variable environment (sometimes unpredictable—Saalfeld and Araújo, 1981), the more rapid the adult stage is achieved, more chances for reproduction occur. Pupal weight does not seem to be influenced by larvae being reared with *P. misera*, *elegans* or *suberosa*.

Acknowledgments. The present investigation received financial support from the Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq) and Pró-Reitoria de Pesquisa e Pós-Graduação (PROPESP), from Universidade Federal do Rio Grande do Sul.

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